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Host distribution, potassium content, water relations and control of two co-occurring mistletoe species

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Abstract

Of 20 tree species available at the Kalamunda Railway Reserve, *Amyema preissii* parasitized all seven *Acacia* species and *Amyema miquelii* parasitized two of 11 *Eucalyptus* species. The host preferences of *Amyema preissii* were confirmed by a germination and establishment experiment on 17 tree species. Larger and older trees tended to bear more mistletoes, within but not between species, and trees closer to neighbours with mistletoes tended to bear more mistletoes, both within and between species, giving a secondary role to bird dispersers in accounting for host preferences.

Both mistletoe species had much higher water and potassium concentrations and transpiration rates than their hosts. Water potential values were also much lower in the mistletoes but the role of water relations in accounting for host specificity appeared of doubtful significance. Minimization of the number of potential hosts, especially *Acacia podalyriaefolia*, appears the most suitable control measure available at present for restricting the spread of these mistletoes.

Introduction

The work reported here is a response to concern by local residents about the rapid spread of mistletoes in the Shire of Kalamunda, Western Australia, and their possible harmful effects on host trees. The study was conducted on the Railway Reserve, starting at the Kalamunda Library and extending northwest as a 40 m band for 1.6 km. This is a remnant of jarrah (*Eucalyptus marginata*) forest which has been thinned in parts and extensively interplanted with ornamental trees indigenous to eastern Australia.

The aim was to record the incidence of mistletoes in relation to identity of mistletoes and host and non-host species, number of mistletoes per tree, tree dimensions and distance from nearest neighbour bearing a mistletoe. Mistletoe seeds were placed on a range of tree species to examine the question of host specificity. Earlier work elsewhere on one of the mistletoe species in the Reserve (*Amyema preissii*) indicated that, of the eight mineral nutrients examined, potassium was in greatest demand relative to supplies from the host (Lamont 1983b, Lamont and Southall 1982 a,b). The potassium drain by the mistletoes on their hosts was therefore examined. It was expected that the water drain would also be considerable (Hellmuth 1971, Lamont and Southall 1982b, Glatzel 1983). The water reservoir in the mistletoe and water content and transpiration rates relative to the host were therefore determined. It has been hypothesized that water potential relations may control host specificity in mistletoes (Lamont 1982) and this was examined here. The distribution data were used as a basis for examining the biological impact of mistletoes in the area and for approaches to reducing their spread.

Materials and methods

Most field work was conducted in autumn, April-May, 1982. Five convenient locations were selected along the Kalamunda Railway Reserve. All trees >3 m high were assessed for number and identity of mistletoes visible from the ground or > 15 cm wide, height (clinometer), diameter at ground level, and closest distance of that tree from a tree bearing a mistletoe (*Amyema miquelii* if it was a eucalypt, *Amyema preissii* if it was another species) until 80 trees were scored.

Whole mistletoes were harvested from the major host species, returned to the laboratory in plastic bags and sorted into leaves, flowers or berries and major (including haustorium) and minor stems and their fresh weight taken. Fresh weights of samples were then obtained, dried at 80°C for at least 48 h, milled and digested with conc. HNO_3. Potassium concentration was determined by flame photometer after addition of La, Cs and HCl (Lamont and Southall 1982a). The process was repeated for leaves and minor stems obtained from the host tree. Total K content of the mistletoe was obtained from the concentration and dry weight figures for each organ. The water reservoir of each mistletoe was calculated in the same way.

Percentage water content was obtained from twigs treated as for whole mistletoes above. Replicate twigs were used for determination of xylem pressure potential (portable pressure bomb) and osmotic potential (sap collected from pressure bomb by filter paper and placed in a sample chamber/microvoltmeter). Other twigs were inserted into Griffin potometers for determination of transpiration rates over 30 min. Canopy temperatures were measured with an air thermister/telethermometer,

Table 1.

Incidence of mistletoe species on 80 trees in relation to potential host species, dimensions and distance from other trees bearing mistletoes. Data are x̄ ± s, where appropriate. Nearest mistletoe (last column) refers to distance of each tree from the nearest tree bearing a mistletoe.

Potential host species	No. trees measured	% with mistle-toes	No. per tree	Maximum No. per tree	Tree height (m)	Tree diameter (cm)	Nearest mistletoe (m)
1. Presence of *Amyema preissii*							
Acacia podalyriaefolia	22	73	7.7	20	5.5 ± 0.9	16.4 ± 6.1	19.4 ± 26.5
Acacia baileyana	5	60	4.2	17	10.6 ± 4.6	32.0 ± 16.0	34.5 ± 42.9
Acacia mearnsii	5	80	1.6	3	8.8 ± 1.7	32.9 ± 21.7	10.7 ± 8.8
Acacia pycnantha	2	100	1.0	1	8.6 ± 1.6	29.5 ± 8.1	10.3 ± 10.3
Acacia decurrens	1	100	1.0	1	8.3	43.0	10.0
2. Presence of *Amyema miquelii*							
Eucalyptus calophylla	24	54	1.8	14	15.6 ± 5.7	57.3 ± 28.0	36.6 ± 38.6
Eucalyptus marginata	8	1	0.1	1	11.7 ± 4.3	62.3 ± 36.0	13.7 ± 6.1
3. Absence of either mistletoe							
Dryandra sessilis	3	0	0	0	4.8 ± 3.2	10.1 ± 3.7	40.9 ± 51.4
Eucalyptus camaldulensis	3	0	0	0	11.2 ± 2.9	43.5 ± 27.2	53.7 ± 40.1
Eucalyptus botryoides	2	0	0	0	8.7 ± 3.9	20.1 ± 15.4	70.0 ± 42.4
Eucalyptus maculata	2	0	0	0	7.4 ± 0.6	17.7 ± 2.4	59.5 ± 57.3
Eucalyptus cladocalyx	1	0	0	0	13.2	22.5	56.0
Eucalyptus astringens	1	0	0	0	11.0	29.0	33.0
Eucalyptus globulus	1	0	0	0	6.6	7.1	50.0

relative humidities by thermohydrograph and wind speed by hand-held or digital anemometers. Leaf areas were determined later with an electronic planimeter and doubled for isobilateral leaves or multiplied by π for terete leaves. Results are means (x̄) ± standard deviations (s) throughout, even though the data did not always fit a normal curve.

Seeds of *Amyema preissii* were squeezed from their berries and placed on the underside of branches 10-40 mm wide. Individual trees of 17 species received 100 seeds each. The number of mistletoe seedlings and leaves per mistletoe were assessed over 60 weeks.

Results

Mistletoe Distribution

Table 1 shows that 51% of trees > 4 m high carried mistletoes at the study site, *Amyema preissii* was borne by 74% of *Acacia* trees and *Amyema miquelii* by 35% of *Eucalyptus* trees. While some plants of all seven *Acacia* species, including *A. longifolia* and *A. saligna* not reported in Table 1, were parasitized, nine of 11 *Eucalyptus* species, including *E. lehmannii*, *E. leucoxylon* and *E. robusta* not in Table 1, possessed no mistletoes. *Acacia podalyriaefolia* was the most heavily infected species with on average 7.7 mature mistletoes per tree up to a maximum of 20. This was followed by *Acacia baileyana* (4.2) and *Eucalyptus calophylla* (1.8). *E. calophylla* was the most common tree at the site (30%), followed by *A. podalyriaefolia* (28%), *E. marginata* (10%), *A. baileyana* and *A. mearnsii* (both 6%).

Apart from *Dryandra sessilis*, few plants of which exceeded 3 m, *A. podalyriaefolia* was the shortest tree (5.5 ± 0.9 m) and had the narrowest trunk diameter (16.4 ± 6.1 cm). Among the eucalypts, *E. calophylla* was much larger (15.6 ± 5.7 m tall, 57.3 ± 28.0 cm trunk diameter) than those species not bearing mistletoes. There was no (non-parametric) correlation between average number of mistletoes per individual and mean distance from the nearest neighbour bearing at least one mistletoe. However, there was a strong negative correlation between the percentage of individuals of each species carrying mistletoes and its mean distance from the nearest mistletoe-bearing neighbour ($p < 0.001$, Spearman's rank). The major exception was *Eucalyptus marginata* where only one of eight trees possessed a mistletoe despite a mean distance of 13.7 ± 6.1 m from the nearest source of *Amyema miquelii*. Trees of *E. calophylla* carried on average over 14 times as many individuals of this mistletoe but were almost three times as far from the nearest source.

Table 2

Variation in dimensions of *Eucalyptus calophylla* and *Acacia podalyriaefolia* trees with and without mistletoes. Data are x̄ ± s. Significances refer to Mann-Whitney tests.

1. *Eucalyptus calophylla*

Amyema miquelii	Present	Absent	Sig.
No. of trees	13	11	—
No. of mistletoes	3.3	0.0	***
Tree height (m)	17.7 ± 6.1	13.1 ± 4.1	***
Tree diameter (cm)	66.8 ± 28.1	46.0 ± 24.4	***
Closest mistletoe (m)	29.4 ± 38.2	45.3 ± 39.0	***

2. *Acacia podalyriaefolia*

Amyema preissii	Present	Absent	Sig.
No. of trees	16	6	—
No. of mistletoes	7.3	0.0	***
Tree height (m)	5.6 ± 0.8	5.2 ± 0.9	NS
Tree diameter (cm)	17.1 ± 0.6	14.5 ± 0.7	***
Closest mistletoe (m)	19.4 ± 29.8	19.2 ± 16.8	NS

Within a species, trees with mistletoes were much larger than those lacking them ($p < 0.001$, Table 2). This association probably did not show up for height of *Acacia podalyriaefolia* because most plants lacking mistletoes were < 3 m, the minimum height for inclusion in the study. Trees of *Eucalyptus calophylla* with mistletoes were much closer to neighbours bearing mistletoes than those without ($p < 0.001$), but this was not true for *A. podalyriaefolia*.

Potassium content

The outermost branches, especially the leaves of both mistletoe species, contained much higher levels of K (Table 3) than equivalent parts of the five host species examined ($p < 0.05$ for minor stems and leaves, Wilcoxon matched-pairs test). There was a gradient

Table 3

Potassium levels in leaves and stems and reproductive parts (when present) of two mistletoe species on five host species at Kalamunda Railway Reserve. Minor stems refer to the outermost branches of the canopy. Units are mg K/g dry tissue. Data are single values or $\bar{x} \pm S$.

Species	Major stems	Minor stems	Leaves	Flowers	Berries	Overall
Eucalyptus calophylla	—	3.6	5.1	—	—	—
Amyema miquelii	3.2	6.3	22.3	17.4	—	9.0
Eucalyptus marginata	—	2.75	2.7	—	—	—
Amyema miquelii	2.25	3.7	16.3	13.5	—	7.0
Acacia podalyriaefolia	—	3.7±2.4	4.0±1.0	—	—	—
Amyema preissii	4.0±1.3	8.6±1.7	15.0±5.2	—	14.9±5.1	11.9±3.9
Acacia pycnantha	—	2.5	5.3	—	—	—
Amyema preissii	7.3	13.6	26.6	—	—	18.7
Acacia decurrens	—	9.0	1.3	—	—	—
Amyema preissii	7.2	13.7	39.0	—	37.6	—

increase of K from the haustorium (major stems) to the leaves, with a slight decrease in the flowers and fruits (including stalks). The overall concentration of K in *Amyema preissii* (15.3 mg g^{-1}) was almost twice that in *Amyema miquelii*. Whole mistletoes represented a K drain on the host of 4.28 ± 8.11 g for *A. preissii* and 5.02 ± 2.87 g for *A. miquelii*. The largest mistletoe collected (*A. preissii* on *Acacia pycnantha*) contained 22.20 g of K.

Water relations

The outermost branches of both mistletoe species consistently contained about 10% higher levels of water (Table 4) than equivalent parts of six host species ($p < 0.05$, Wilcoxon matched-pairs test). Whole mistletoes contained 49.0 ± 10.6% water, which represented a water volume of 1.77 ± 3.06 l in a total weight of 4.19 ± 7.69 kg for both species. The largest mistletoe collected (*Amyema preissii* on *Acacia pycnantha*) weighed 19.78 kg and contained 7.91 l of water. Xylem pressure potential (ψ_x) was consistently much lower in the mistletoes than in the six host species examined ($p < 0.05$, Wilcoxon). The osmotic potential of extracted sap (ψ_o) was also lower in the mistletoes ($p < 0.05$, Wilcoxon).

Table 4

Water content, xylem pressure and osmotic potentials of twigs of two mistletoe species and six host species. Data are $\bar{x} \pm s$. Negative signs are omitted from potential values.

Species	Water content (%)	ψ_x (bar)	ψ_o (bar)
Eucalyptus calophylla	51.4	10.8±3.8	3.4±2.0
Ameyema miquelii	59.9	13.8±9.7	3.7±2.3
Acacia podalyriaefolia	46.2±7.0	17.9±3.4	4.8±1.8
Amyema preissii	56.6±6.6	23.6±2.2	5.5±1.6
Acacia pycnantha	59.7±9.8	9.9±2.7	2.6±1.8
Amyema preissii	72.5±14.4	17.5±12.0	4.4±1.4
Acacia baileyana	57.5±16.0	12.1±12.6	4.6±3.2
Amyema preissii	70.9±9.1	19.1±18.2	6.2±4.0
Acacia mearnsii	55.3±5.5	9.1±3.8	5.4±2.4
Amyema preissii	62.3±3.4	13.6±2.3	4.4+0.3
Acacia decurrens	63.6	7.8	3.0
Amyema preissii	70.8	9.6	4.5

Table 5

Comparison of water relations between *Eucalyptus calophylla* with and without mistletoes and other *Eucalyptus* species lacking mistletoes. Results are ranges. Negative signs omitted from potential values. Sig. refers to Mann-Whitney tests.

Tree species	Mistletoes	Water content (%)	ψ_x (bar)	ψ_o (bar)
A. *Eucalyptus calophylla*	present	51.4	5.5-14.6	2.2-6.4
B. *Eucalyptus calophylla*	absent	50.3-58.4	5.2	2.3
C. 6 *Eucalyptus* Spp.	absent	38.3-66.6	7.2-21.4	1.7-7.3
Sig. (A v C)		—	**	NS

There was no difference apparent in % water, ψ_x and ψ_o between the trees of *Eucalyptus calophylla* with and without mistletoes (Table 5). However, there was a tendency for the other (non-host) eucalypt species to have lower ψ_x values than *E. calophylla* ($p < 0.01$, Mann-Whitney test), but no differences in % water or ψ_o.

Except for *Eucalyptus marginata*, the other six host species had much lower rates of transpiration (Table 6) than the two mistletoe species ($p < 0.05$, Wilcoxon matched-pairs test). Omitting *Amyema miquelii* on *E. marginata*, whole mistletoes lost 29.43 ± 30.07 ml water per hour from 10.00 to 15.00 h over the two days measurements were taken. Conditions were overcast, rain falling overnight though insufficient to moisten the dry surface soil. Host canopy temperature averaged 23°C (range 14.2-28.4°C), relative humidity 73% (range 58-100%) and windspeed 1.2 m s^{-1} (0-2.5 m s^{-1}).

Host specificity

Of the 1700 seed of *Amyema preissii* removed manually from their berries and placed on the various tree branches, 93.1 ± 5.7% germinated. By eight weeks, the adhesive pad of almost all germinants was fixed to the bark (Table 7). By 28 weeks, this had fallen markedly on most host species and by 60 weeks, no seedlings remained alive on all 10 *Eucalyptus* species and *Dryandra sessilis*. Some seedlings were still alive and growing vigorously on all five *Acacia* species while most seedlings were barely alive on *Nuytsia floribunda*. *Amyema preissii* was most successful on *Acacia podalyriaefolia*, with 72% establishment and 58 ± 70 leaves after 60 weeks.

Table 6.

Transpiration rates of twigs of two mistletoe species and seven host species. Rates on a leaf area basis. Data are x̄ ± s. Significances refer to analyses of variance.

Species	Unit transpiration ($ml\ m^{-2}\ h^{-1}$)	Sig.	Total transpiration ($ml\ h^{-1}$)
Eucalyptus calophylla	12.48±7.00		
Amyema miquelii ...	34.44±9.74	*	31.87±3.40
Eucalyptus marginata...........	38.88		
Amyema miquelii ...	8.10	—	1.92
Acacia podalyriaefolia	34.74±26.52		
Amyema preissii	82.80±45.21	*	6.79±3.08
Acacia baileyana.....	15.90		
Amyema preissii	21.24	—	111.18
Acacia mearnsii	19.80		
Amyema preissii	140.4	—	35.70
Acacia decurrens	29.34±23.40		
Amyema preissii	130.80±42.42	***	17.72±17.08
Acacia pycnantha....	4.44		
Acacia preissii	58.50	—	50.18

Table 7

Number of seedlings of the mistletoe *Amyema preissii* which were attached to 17 tree species over 60 weeks at Kalamunda Railway Reserve. 100 seeds were placed on each tree. Leaves per mistletoe are x̄ ± s.

Tree species	8 weeks	28 weeks	60 weeks	Leaves/mistletoe
Acacia baileyana+	81	1	1	40
Acacia decurrens+	85	10	5	52±38
Acacia mearnsii+	97	8	5	72±24
Acacia podalyriaefolia+.....	96	72	72	58±70
Acacia pycnantha+	95	7	2	6
Dryandra sessilis#	100	27	0	—
Eucalyptus astringens.	91	0*	0	—
Eucalyptus botryoides.	90	8	0	—
Eucalyptus calophylla#.............	100	42	0*	—
Eucalyptus camaldulensis	80	26	0*	—
Eucalyptus cladocalyx	66	6*	0	—
Eucalyptus globulus....	94	26	0*	—
Eucalyptus lehmannii.	95	22	0*	—
Eucalyptus leucoxylon..............	100	36	0*	—
Eucalyptus marginata#	89	59	0	—
Eucalyptus robusta	90	51	0	—
Nuytsia floribunda#....	100	78	60	1 ± 1

\+ Usual host of *Amyema preissii* at study site.

\# Species occurs naturally, rest planted by Kalamunda Shire Council.

* Flaking of host bark could have contributed to failure of attachment.

Discussion

Inspection of 20 potential host species showed that *Amyema preissii* parasitized all and only *Acacia* species, while *Amyema miquelii* was almost confined to one of the 11 *Eucalyptus* species available. This apparent host specificity was confirmed by placing seed of *Amyema preissii* on 17 tree species: all germinants died except those on *Acacia* species. The single exception was tenuous growth on *Nuytsia floribunda*—an induced example of epiparasitism, as this species is a root hemiparasite. Seed of *Amyema miquelii* was unavailable so the ability of this species to parasitize eucalypts in general remains unresolved. In contrast to *E. calophylla*, it showed almost no affinity for *E. marginata* (one tree on the entire Reserve) but *Amyema miquelii* has been recorded on a wide range of eucalypts elsewhere (Barlow 1966).

From these considerations, host preferences of the two mistletoe species appear much more important than perching preferences of bird dispersal agents in accounting for the spread of mistletoes (c.f. Lamont and Perry 1977, Lamont 1983a). If birds were limiting their spread, it could be hypothesised that the larger species and those trees closer to already infected hosts would carry greater loads of mistletoes. In fact, one of the smallest species, *Acacia podalyriaefolia*, was most heavily infected and percentage establishment in the host-specificity experiment was greatest for this species. Within species, only the largest individuals carried mistletoes. This is clearly a function of plant age rather than bird preferences; establishment of mistletoes on susceptible species is time-dependent. However, trees, both within (Table 1) and between (Table 2) species, which were closer to neighbours bearing mistletoes tended themselves to carry a greater mistletoe load. This can be related to the increased probability of receiving seeds from birds after visiting infected trees.

In comparison with their hosts, the two mistletoe species contained larger amounts of water and nutrients (potassium) on a unit weight basis. Apart from the inert mass of each mistletoe (mean 4.19 kg) to be supported by the host, whole mistletoes contained on average 1.77 l water and 4-5 g K. These mistletoes also lost considerable amounts of water, whole plants transpiring on average 29.4 ml per daylight hour during mild autumn weather. Despite these drains on the host's resources, only *Acacia podalyriaefolia* showed obvious signs of retarded growth and the mistletoe load could have contributed to the 9% of its individuals which were dead at the study site. Infected trees were in fact larger than uninfected trees because they were older (contrast Lamont and Southall 1982b).

Sap flow is maintained by water potential gradients so that it is understandable that the potentials for the two mistletoes were usually much lower than those of their hosts' (Table 4). This requirement suggests that host specificity may be related to the water potential properties of mistletoe and potential host (Lamont 1982). This possibility is given limited support by the observation that the xylem potential values of non-host *Eucalyptus* species were usually lower than those of the host species *E. calophylla* (Table 5). However, this would need to be tested experimentally, as ψ_x ranged widely for *Amyema preissii* on different hosts (Table 4) and it still did not parasitize *Eucalyptus* species with much higher ψ_x values than recorded for itself. The present data do not give clear support to the role of water relations in determining host specificity.

There does not seem to be a simple solution to the control of these mistletoes. Plants that were broken back to the haustorium resprouted readily from submerged tissue in the haustorium. Death is only assured by cutting the host stem beneath the haustorium, an especially difficult task for *Amyema miquelii* located up to a height of 20 m on *Eucalyptus calophylla*.

In terms of possible biological control, the White Wax Scale, *Gascardia destructor*, was widespread on *Amyema preissii*. However, plants with the scale did not appear greatly affected (they may even have increased the water and nutrient demand on the host) and it has a wide host range, especially citrus. Occasional plants of *A. preissii* were heavily grazed, presumably by larvae of the Mistletoe Butterfly, *Ogyris amaryllis* or a close relative (pers. obs., Atsatt 1981). This group has the advantage of monophagy and numbers could be built up for release in the area. However, the mistletoes would recover by resprouting during any population crashes of the butterfly. Possums (*Trichosurus* spp.) are considered a major predator on mistletoes in Australia (Barlow 1981) and are still present in Kalamunda. They would provide the most effective control by preventing flowering and fruit set but they are unacceptable in residential areas.

The final avenue is choice of species for future planting programmes. Reduction of suitable hosts would follow the removal of, or planting trees other than *Acacia* species, especially *A. podalyriaefolia. Amyema preissii* is not indigenous to the area and was probably introduced via cultivated *Acacia* species. Alternatively, susceptible species should be planted at least 100 m apart (Table 1). A particular problem with *A. podalyriaefolia* is that it naturalizes readily and soon builds up a vulnerable population of trees. *Eucalyptus* and other indigenous and exotic genera beside *Acacia* do not appear to be very prone to mistletoes. Even *Eucalyptus calophylla*, the dominant tree on the Reserve and the species with longest exposure to mistletoes, only carried an average load of $<$ 2 mistletoes per tree. However, continued thinning of the population by urban development and lack of recruitment of young plants will lead to an increase in the mistletoe load per tree over time (Table 2, Lamont and Southall 1982b).

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